A First Mathematical Model of Brood Sorting by Ants: Functional Self-Organization Without Swarm-Intelligence.

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Brood sorting, observed in *leptothorax unifasciatus* ant colonies, is a major example of social insects ability to solve problems at the collective level. Two processes characterize this phenomenon: a process of aggregation of all brood items in a single cluster, coupled with a process of segregation of items in concentric annuli, each containing items of different type, and ordered such a way that the smallest items are at the center, the largest at the periphery, and prepupæ dispersed in-between.

In spite of its influence on algorithmics and robotics methods, no formal explanation of the brood sorting phenomenon was ever given. We present a first mathematical model devoted to brood sorting. Our hypothesis about ants behaviour are consciously minimal: we assume that random rules their acts, not only when they walk but also when they choose a brood item that they pick up, or beside which they deposit the one they carry. The first part of our work deals with the process of aggregation in a single cluster. The main subject of our study is the time evolution of a mathematical function linked to the notion of cluster. We prove that, whatever the number of ants acting, this function tends to decrease until it reaches a threshold that we compute: this threshold matches with the formation of the single cluster. The second part of our work deals with segregation in concentric annuli. Coupling the concept of virtual size of a brood item to the previous conclusions leads to a realistic explanation of the concentric structure observed in ant colonies.

Finally, we prove the existence of a feed-back effect, so that our results suggest that brood sorting is a case of self-organization that does not involve swarm intelligence.

1. Introduction

Social insects are well known for their ability to build spatial complex structures: cite, for instance, nest building (Jeanne, 1975; Grassé, 1984) brood sorting (Franks and Sendova-Franks, 1992) or population self-sorting (Sendova-Franks and Franks, 2004; Backen et al., 2000; Sendova-Franks and van Lent, 2002). These constructions are widely considered as resulting from collective work: indeed, it seems unlikely that each individual has a precise idea of the structure under construction. This ability to solve problems at the collective level is named collective -or swarm- intelligence (Camazine et al., 2001); the concept of stigmergy is also used when an individual reacts to modifications of its environment due to the action of an other individual (Grassé, 1959; Bonabeau et al., 1999).

Brood sorting, observed in ant colonies, e.g. *lasius niger* (Depickére et al., 2004), *leptothorax* (Franks and Sendova-Franks, 1992), *Pheidole pallidula* or *Messor sancta* as reported by Deneubourg et al. (1991), is one of the main examples of collective intelligence. Such ant colonies organize their brood in a single cluster. In *leptothorax unifasciatus* ant colonies, the brood cluster is made up of concentric annuli, each containing items of a different type, with the youngest items (eggs and micro-larvæ) gathered at the center, and successively larger larvæ arranged in increasingly wider spaced bands moving out from the center of the cluster (Franks and Sendova-Franks, 1992). It is noteworthy that this annular structure ensures that the most evolved brood items are fed first (Franks and Sendova-Franks, 1992).

Brood sorting, as well as other social insect

buildings, stresses the complexity of relationship between individual and collective behaviors. For this reason mainly, it has influenced the development of research domains, such as ants algorithms (e.g. Lumer and Faieta, 1994; Kuntz et al., 1999) or collective minimalist robotics (e.g. Melhuish et al., 2001).

Several models have been proposed in order to explain the brood sorting phenomenon: Deneubourg et al. (1991) presented a first cellular automata model devoted to cemetery formation in ant colonies, also available for the process of aggregation in a single cluster in the case of brood sorting. In this algorithmic model, ants move randomly and are assumed to recognize items of different types and to estimate their density in the immediate neighborhood. An item is more probable to be picked up (resp. put down) if the number of immediate neighbors of the same kind is small (resp. large).

Martin et al. (2002) revisited this cellular automata model and showed, by means of simulations, that the task of aggregation was accomplished, only a bit slower, without the need to bias the pick up and deposition probabilities and with only one agent.

As regards the phenomenon of segregation in concentric annuli observed in *leptothorax* ant colonies, two physical models where used for an explanation: firstly the differential adhesion model (Steinberg, 1963), involving concentric spheres so as to explain the sorting out of adhering cells of the same type during morphogenesis; secondly, the muesli effect (Barker and Grimson, 1990) is a model for self-sorting by size which occurs under the influence of shaking and gravity.

More recently, Franks and Sendova-Franks (1992) studied brood sorting in *leptothorax* ant colonies, and tested the hypothesis that the sorting is made up of two phases: the clustering of all brood items together constitutes a first phase, followed by a second phase in which a mechanism of differential diffusion leads to the formation of concentric annuli where items of different type take their relative positions. The method was experimental and statistical.

However, to our knowledge, no formal explanation was ever given, neither for aggregation in a single cluster, nor for segregation in concentric annuli. This article presents a first mathematical model devoted to brood sorting.

In the first part, we deal with the phenomenon of aggregation. Our hypothesis are quite minimal: ants are only assumed to recognize brood items (say larvæ), but ignore each other, and have no notion of density. Walking randomly, they pick up a larva which is not carried by another ant (such a larva is said free), and deposit this larva beside an other free larva, precisely randomly in a disk which center is the free larva. We build an algorithmic model for simulations, and we establish mathematical results giving properties of a stochastic process which is the average of squared distances between larvæ. By means of probability theory, we prove that this process decreases -in average-, until it reaches a threshold that we compute: this threshold matches with the formation of the single cluster. Once this cluster has been formed, the process oscillates around the threshold, with a standard deviation that we also compute. Therefore, one can consider that the brood aggregation is a natural minimization of the average of squared distances between larvæ. An important fact is that this result is also available in the case where a single ant is involved.

-In the second part, we use results of the first part to deal with brood geometry and give an explanation of concentric annular sorting in the case of different types of larvæ. We combine numerical methods of minimization of the average of squared distances between larvæ and mathematical proofs, and introduce the notion of virtual size of a brood item, which takes into account the care it needs. Therefore, we get a realistic explanation of the geometric structure observed in *leptothorax* ant colonies.

Our results tend to prove that in the case of brood sorting, the concept of collective -or swarm- intelligence is out of use. We claim that it is rather a case of self-organization, or functional emergence, in the sense that annular sorting is a natural and involuntary construction which appears as the most profitable.

2. Aggregation

This section is devoted to the mechanism underlying the phenomenon of aggregation of items in a single cluster, observed both in cemetery formation and brood sorting. We first present our mathematical model, before exposing the results it involves. Here, brood items are assumed to be undifferentiated and we name them larvæ.

2.1. Model definition

2.1.1. A preliminary enlightening result

Martin et al. (2002) have proposed, as the main reason for single cluster formation, the fact that once a cluster has vanished, it can't reappear. Even if this phenomenon is of major importance in aggregation dynamics, it is true in a single abstract and ideal case, *i.e.* when larvæ are material points and when a larva is deposited exactly upon another. In this case, the concept of cluster is well defined and we easily prove that only one cluster will remain: indeed, assume the brood is made up of N larvæ, distributed in m initial clusters, with $m \leq N$. Let

$$X^n = (X_1^n, \ldots, X_m^n)$$

be the random vector containing the number of larvæ in each cluster at time n (i-th cluster contains X_i^n larvæ). X^n is a Markov chain, the state space is $[0, N]^m$ and for the sake of concision, we suppose that the transition matrix is independent of n. The transition probabilities are assigned to events of type "one larva is displaced from cluster i to cluster j". Since an empty cluster cannot receive any larva, there are exactly m absorbing states $(N, 0, \ldots, 0), \ldots, (0, \ldots, 0, N)$, each state corresponding to a configuration with only one cluster. Given that the state space is finite, the Markov chain must eventually enter one of those absorbing states (and remain in this state). Thus, almost surely, a single and persistent cluster is formed.

However, as soon as larvæ are not material points, and since a given larva is deposited beside an other (but not exactly at the same place), clusters may be broken and the model proposed by Martin et al. (2002) is not relevant anymore.

The mathematical model of the brood-sorting algorithm we have built is inspired by a classical computer model developed in our laboratory. It is a Markov chain for which states are positions of larvæ which constitute the brood (therefore the state space is neither finite, nor discrete). It's a discrete-time stochastic process, since positions are updated only when one larva is picked-up or released by one ant.

2.1.2. General framework

Let us describe the state space of our process. To each larva we assign the vector of its position in the plane, so that we consider a larva as "temporarily vanished" when carried by an ant. This state is indicated by the symbol $\star$. Therefore, if N is the number of larvæ, the list of all positions can be written:

$$V = (V_1, \ldots, V_N) \in E = \left(\widetilde{\mathbb{R}^2}\right)^N$$

where $\widetilde{\mathbb{R}^2}$ stands for $\mathbb{R}^2 \cup \{\star\}$. For $V \in E$ we define the number of larvæ on the ground, *i.e.* which are not carried by an ant:

$$C(V) = \text{card}\{i, V_i \neq \star\}$$

2.1.3. Dynamics of brood sorting

Now we define the functions that represent the possible transitions of the process. The action of picking the k-th larva, when applied to vector V, gives $R_k(V) = W$ with

$$W_i = V_i \quad \text{for } i \neq k \quad \text{and} \quad W_k = \star$$

The action of putting down the k-th larva beside the l-th one is defined as follows. Our computer model assumes that even if larvæ are immaterial, ants release them beside ananother larva. In order to take this fact into account, we consider a random vector ε, with uniform distribution in the disk $D(0, \delta)$, $\delta > 0$ (note that all this work could be done with any other radial distribution). Each time a larva is released beside another one, the vector ε stands for such a random vector, independent from all other variables. Applied to a vector V, this transformation gives ${}^{\varepsilon}D_{kl}(V) = W$ with:

$$W_i = V_i \quad \text{for } i \neq k \quad \text{and} \quad W_k = V_l + \varepsilon$$

So that $W_k - W_l = \varepsilon$.

We must point out that actions R_k and ${}^{\varepsilon}D_{kl}$ are

not exactly defined on E, since R_k can only be applied to a list V for which $V_k \neq \star$, and ${}^{\varepsilon}D_{kl}$ needs $V_k = \star$ and $V_l \neq \star$ to be applied to V. Nevertheless, this fact is not problematical and makes notations more convenient.
Now we define the stochastic process. Time steps will be denoted by n at exponent.

We state that at time n, all the actions that are allowed (depending on the state at time n) have even chances to happen (this is an approximation of what actually happens, but it is relevant for the brood surface is finite). Successive actions, denoted by $M^1, M^2, \ldots, M^n, \ldots$ are applied from the initial state of the process V^0:

$$V^n = M^{n-1}(V^{n-1}) = M^{n-1} \circ \ldots \circ M^1 \circ M^0(V^0)$$

2.1.4. The process

Finally, we define the function on E that will express the dispersion among the brood: this function gives the average of squared distances between free larvæ, that is,

$$S(V) = \frac{\sum_{i,j \neq \star} \|V_i - V_j\|_2^2}{C(V)(C(V)-1)}$$

We first have the following result (we recall that the expression "almost surely" means "with probability 1"):

Proposition 2.1 ***Almost surely, the process*** $S(V^n)$ ***reaches a value lower than*** $s\left(2 - \frac{1}{N}\right)$.

This result suffices to prove the phenomenon of aggregation, since this low value for $S(V^n)$ forces the larvæ to be in a "single cluster" configuration.

Moreover, we want to know if those cluster configurations are statistical accidents, or if they are stable. In order to answer this question, we will study, in the following section, the conditional expectation of the process. This way, we will show that, in some statistical sense, "small clusters" can't be broken.

2.2. Conditional Behavior

We now compute the conditional expectation of our process. The number of ants is denoted by F. The assumption made about the choice of a larva to be picked up or deposited allows us to define $C(V^n)$ as a Markov chain: put

$$\begin{aligned}\lambda_k &= \mathbb{P}(C(V^{n+1}) = k+1 | C(V^n) = k) \\ &= 1 - \mathbb{P}(C(V^{n+1}) = k-1 | C(V^n) = k)\end{aligned}$$

Thus, for the sake of concision, we write

$$a(k) = \frac{2\lambda_k}{k(k+1)} \quad \text{and} \quad b(k) = \delta^2 \frac{\lambda_k}{k+1}$$

the main result exhibits the conditional dynamics of our process:

Proposition 2.2

$$\begin{aligned}&\mathbb{E}\left[S\left(V^{n+1}\right) \middle| V^n\right] \\ &= \left(1 - a(C(V^n))\right) S(V^n) + b(C(V^n))\end{aligned} \tag{1}$$

Observing proposition 2.2, we see that the number of ants acting in the brood has a narrow influence on the behavior of $S(V^n)$. Thus, we first study the single ant case, and then we generalize to the several ants process.

2.3. Single ant process

If we assume that at time 0, all larvæ lie on the ground, when a single ant acts on the brood, since operations of picking a larva and putting it down both happen cyclically, we notice that $C(V^{2n}) = N$ and $C(V^{2n+1}) = N-1$. Therefore, considering processes $S\left(V^{2n}\right)$ and $S\left(V^{2n+1}\right)$ leads to useful simplifications. Proposition (2.2) becomes:

Proposition 2.3 *If* $F = 1$ *process* $S(V^n)$ *satisfies (for* $i = 0, 1$*):*

$$\begin{aligned}&\mathbb{E}\left[S\left(V^{2(n+1)+i}\right) \middle| V^{2n+i}\right] \\ &= \left(1 - \tfrac{2}{N(N-1)}\right) S(V^{2n+i}) + \tfrac{\delta^2}{N}\end{aligned} \tag{2}$$

Writing $\theta = \frac{N-1}{2}\delta^2$, equation (2) gives some intuitions that we will develop in proposition 2.5: at even times, our process behaves like a sub-martingale when $S(V^{2n}) \leq \theta$, otherwise it behaves like a super-martingale (the same is true for odd times). We conclude that the process is, in a sense, attracted by the value θ, which we call pulsation threshold. First, the limit of the expectation of the process, when time step n tends to infinity, can be computed for even and odd times and gives the same result:

Proposition 2.4

$$\lim_{n\to+\infty} \mathbb{E}\left[S(V^n)\right] = \theta$$

Therefore, the brood is expected to concentrate until it reaches the pulsation threshold and then to oscillate around this threshold. The limit value θ is small enough to avoid dispersion of the brood, so that this result confirms the fact that once a single cluster configuration has been reached, the probability to escape from this configuration is weak. In order to make this result more precise and to confirm the expected behavior of $S(V^n)$, we give a result similar to some used to prove up-crossing inequalities:

Proposition 2.5 *Let $\tau_1 \leq \tau_2 \leq m$ two bounded stopping times (adapted to the natural filtration associated to the process V^n), then:*

$$S(V^{\tau_2}) \geq \frac{b}{a} \quad \Rightarrow \quad \mathbb{E}\left[S(V^{\tau_2})|\, V^{\tau_1}\right] \leq S(V^{\tau_1})$$

and

$$S(V^{\tau_2}) \leq \frac{b}{a} \quad \Rightarrow \quad \mathbb{E}\left[S(V^{\tau_2})|\, V^{\tau_1}\right] \geq S(V^{\tau_1})$$

Area $\left[\frac{b}{a}, +\infty\right[$ is what we call a "decreasing area" for the process, while $\left]0, \frac{b}{a}\right]$ which is an "increasing area". Therefore, proposition 2.5 confirms intuition: both decreasing an increasing area are expected to be unstable for $S(V^n)$ and to push the process near the value θ.
Nevertheless, this does not mean that the process has a limit. First, as the process can be supposed to be bounded (this doesn't change significantly the previous results), we assume that $S(V^n)$ is uniformly integrable, and then deduce that **the first time** (and then the following ones) **the process goes through the threshold θ isn't bounded**. Moreover, here are two results that deal with asymptotic behavior of $S(V^n)$. First, we show that the process will eventually oscillate around θ:

Proposition 2.6 *Denote by* $\mathrm{Var}(S(V^n))$ *the process variance at time n. We have:*

$$\lim_{n\to+\infty} \mathrm{Var}(S(V^n)) = \nu_N > 0$$

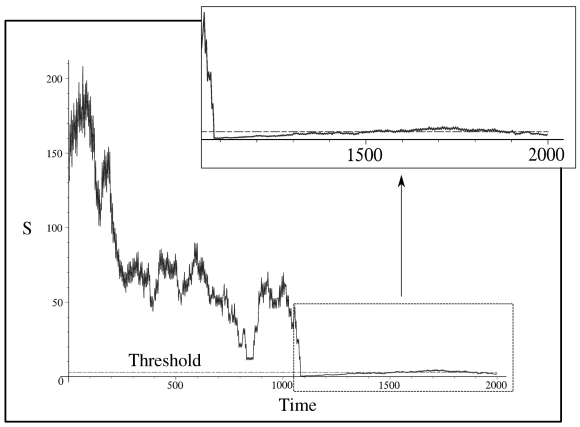

Figure 1. Simulation with 1 ant and 25 larvæ

The formula defining ν_N is too big to be exposed here, but the crucial point is that $\nu_N > 0$. In order to see that this variance isn't negligible, we give an approximation of ν for large values of N:

$$\nu_N \approx \frac{N^3}{3} s^4$$

So, the process cannot converge to θ, moreover, using Markov chain theory we can prove the stronger result:

Proposition 2.7 *$S(V^n)$ cannot converge in L^1 to any random variable.*

Finally, summarizing our results, we can conclude that the process, even if attracted by the value θ, will oscillate forever near it, as if some kind of elasticity was operating (see fig. 1). In the next section, we show how, under supplementary hypothesis, we extend those results to the general case.

2.4. Several ants process

As in the single case, and since Markov chain $C(V^n)$ is 2-periodic, we concentrate on the two sub-processes $S(V^{2n})$ and $S(V^{2n+1})$. In order to extend proposition 2.4 to the multiple ants process, we need to assume that $C(V^n)$ and $S(V^n)$ are independent random variables. Relevance of this hypothesis comes from the fact that we consider the mean of squared distances, which seems

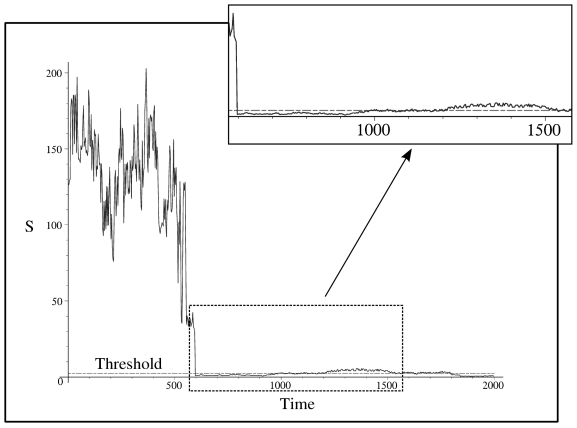

Figure 2. Simulation with 8 ants and 25 larvæ

to be, as n grows, independent from the number of larvæ on the ground. Under this assumption we get the following result:

Proposition 2.8 *There exists two real numbers θ_e and θ_o such that:*

$$\lim_{n\to+\infty} \mathbb{E}\left[S\left(V^{2n}\right)\right] = \theta_e$$

$$\lim_{n\to+\infty} \mathbb{E}\left[S\left(V^{2n+1}\right)\right] = \theta_o$$

Let X be a random variable with binomial distribution $\mathcal{B}\left(F, \frac{1}{2}\right)$, and $Y = X + N - F$, then for large values of N:

$$\theta_e \approx_N \theta_o \approx_N \frac{\mathbb{E}\left[a\left(X + N - F\right)\right]}{\mathbb{E}\left[b\left(X + N - F\right)\right]}$$

Remark 1 Even if the values θ_e and θ_o are easily computed, the approximation of those thresholds arises naturally and suffices to highlight similarities with the single ant case.

Again, the threshold can be observed on simulations (see figure 2). The result about the variance of the processus is analogous to the one obtained in the single ant case, but the formula is too heavy, so we won't write it. Nevertheless, it is important to notice that the mean square root has the same order of magnitude that the mean: as the number of ant is constant, the mean square root behaves like $\frac{\sqrt{7}}{6}N\delta^2$ when N grows. Regarding conditional dynamics, we can easily bind the process with a process with $F = 1$, but the best way to think of the variability of several ants case is to notice that, according to the value of $C(V^n)$, the process behaves like a single ant process, so it will jump between different single ant processes with respectively $N - F, N - F + 1, \ldots$ and N larvæ. This is why we can guess on simulations a bigger variance (this is confirmed by the formula we obtained.)

2.5. Conclusions on aggregation

We have proved that the process $S(V^n)$ is not really affected by the number of ants working in the brood. Furthermore, considering equation (2.2) leads us to the conclusions that the dynamics of the brood, and the speed (in terms of logical time) of cluster formation are similar (however, in terms of real time, obviously many ants sort the brood much faster than a single worker; in fact, this is the only relevant collective effect). Then, it becomes clear that the nature of the phenomenon of aggregation remains unchanged as the number of ants varies. We can go further in the analysis of our results and extract an important feature: we have highlighted the fact that, in the phenomenon of aggregation, collective action of ants is similar to a stochastic algorithm minimizing the sum of distances between larvæ. In the next section, we use this fact in order to deduce results with regard to the phenomenon of segregation.

3. Segregation

Hartmann (2005), O'Toolenw et al. (2003), Franks and Sendova-Franks (1992) and others, studied the following question: why is the brood arranged in concentric annuli, with eggs at the center and larger larvæ at the periphery? Wilson et al. (2004) propose two hypothesis: the first one was made by analogy with the manner in which muesli settles in transit. The phenomenon of smaller clusters falling to the bottom, leaving the larger ones on top has been studied by Barker and Grimson (1990). This analogy was made con-

sidering that instead of gravity, larvæ move as if they were attracted by a centripetal force that could cause the same effect on segregation. Under this hypothesis, annular sorting is a consequence of differences between sizes of larvæ. Unfortunately, after simulations, Wilson et al. (2004) concluded that using objects of different sizes doesn't lead to efficient sorting in the brood. Another hypothesis is that ants deliberately introduce spacing between brood items. The extent of spacing is influenced by the size of the brood item, detected by the amount of waste gas the brood item produces. A spacing mechanism has been explored using real robots (Melhuish et al., 1998) and produced one central circle with a concentric ring around the outside. However, Melhuish et al. (1998) tested this mechanism with only two types of objects of the same size.

All these hypothesis couldn't lead to satisfying experiments and simulations; therefore, works have been achieved in order to improve annular sorting, acting on criteria which make ants decide whether they set down the larva they carry or not. This was justified by the fact that mature larvæ need more care than young ones and being placed at the periphery, ants approach them more easily. Implicitly, this explanation involves the notion of collective aim and assumes that ants are able to recognize annular configurations which is not obvious.

In section 2 we proved that there is no need, in our model, to invoke collective intelligence. In this section, we adapt the two hypothesis put forth by Wilson et al. (2004) in the light of our results: we combine them in order to explain annular sorting as a consequence of local activity.

In this section, we first precise the hypothesis of attraction that ensures our minimization principle; subsequently, we present mathematical results explaining the natural emergence of annular configurations.

3.1. Mutual attraction

In section 2, we concluded that -according to our model- the collective action of ants imitates a stochastic algorithm that minimizes the function S. Under this hypothesis, we can go further in the insight of brood's dynamics. Rather than a centripetal force, as proposed by Wilson et al. (2004), our results confirm formally that this dynamics results from mutual attractions between larvæ (Bonabeau et al., 1999). However, in all models, this dynamics is distorted by stochastic behaviors, so that it isn't easily observed. Dropping the stochastic part of the model, we only have to study the abstract case in which ants collectively reach a minimal state for S. The question is thereby: which configurations minimize S? Let's formalize this problem: larvæ are assimilated to disks in the plane, that is

- $V = (V_1, \ldots, V_N)$ are the coordinates of their centers
- $(r_1, \ldots, r_N)$ the list of their radius.

We impose the natural constraints:

$$D(V_i, r_i) \cap D(V_j, r_j) = \emptyset \quad \forall i, j \tag{3}$$

where $D(V_i, r_i)$ denotes the disk with center V_i and radius r_i. Now we want to bind annular configurations of V to the ones that minimize $S(V)$.

3.2. Annular configurations minimize S

Numerical simulations clearly illustrate the fact that minimal configurations for $S(V)$ match annular ones. Figures 3 and 4 give two examples of numerical optimizations we obtained.

In order to understand this phenomenon, we propose a simple explanation supported by mathematical results. The idea is that, if one increases the size of a larva, say V_1, it will move away larvæ stuck on both sides of V_1, so that if V_1 is at the periphery of the cluster, its growth won't move away many larvæ, and won't increase $S(V)$ to a significant degree.

In order to deal rigorously with this idea, we first define the transformation that captures the increase of a radius. Precisely, as a first approximation, we consider that increasing radius r_k by $\lambda > 0$ leads to push forward, in straight line, all other larvæ. The function involved can be defined as:

$$H_{\lambda,k}(V) = \Big(V_1 + \lambda \tfrac{V_1 - V_k}{\|V_1 - V_k\|}, \ldots, V_k, \ldots, V_N + \lambda \tfrac{V_N - V_k}{\|V_N - V_k\|}\Big)$$

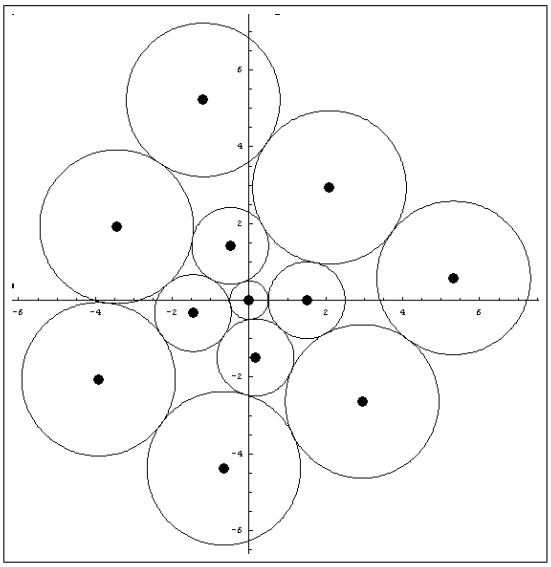

Figure 3. Numerical minimization of S: case of 1 small larva, 4 intermediate and 7 large larvæ

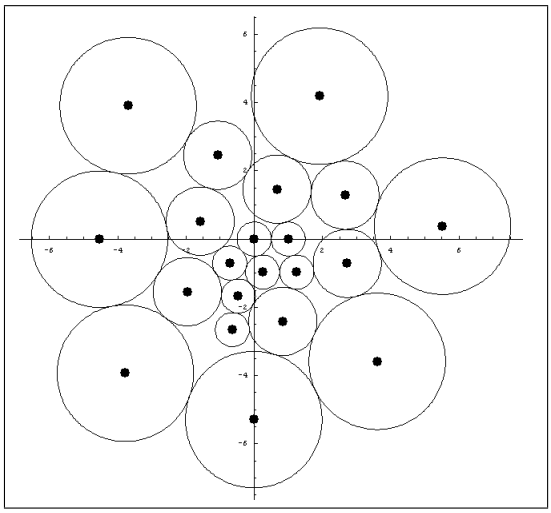

Figure 4. Numerical minimization of S: case of 7 small larvæ, 7 intermediate and 7 large

Obviously, this function does not preserve minimalism for S, nevertheless, we want to study the effect of infinitesimal increase to detect where big larvæ are expected to be in a minimal configuration. The function H is then sufficient to find this kind of information. We define the penalization function:

Definition 3.1 *The penalization function of S by the disk D_k is:*

$$P_{S,k}(V) = \frac{d}{d\lambda} S(H_{\lambda,k}(V))|_{\lambda=0}$$

In a minimal configuration, disks with high penalization values on S, according to their positions, are expected to be the smallest among other disks, and conversely. Writing α_i^k the angle between vector $V_i - V_k$ and the absissa axe, we prove that:

Proposition 3.1 *Penalization $P_{S,k}$ by D_k satisfies:*

$$P_{S,k}(V) = 4 \sum_{i \neq k} \|V_i - V_k\| \left[N - \tfrac{1}{2} - \sum_{j \neq k} \cos\left(\alpha_i^k - \alpha_j^k\right) \right]$$

This result confirms our intuition: the contribution of two disks, say D_i and D_j, to the penalization by D_k decreases with the distance $|\alpha_i^k - \alpha_j^k|$. Therefore, any peripheral disk will cause a low penalization of S, we can precise this idea by using the notion of field of view:

Definition 3.2 *The field of view of a disk D_k is the smaller real $\alpha_k \in [0, \Pi]$ such that there exists a closed angular sector $S(V_k, \alpha)$, with center V_k and angle α_k, satisfying:*

$$V_i \in S(V_k, \alpha) \quad \forall i = 1..N$$

Disk with low FoV are not surrounded by other disks, they must have a peripheral position (see examples on Fig. 5 and 6). Finally, the following result makes a clear link between FoV and penalization

Corollary 3.1 *The penalization of D_k on S satisfy:*

$$P_{S,k}(V) \leq 4 \left[N - \frac{1}{2} - \cos(\alpha_k^k) \right] \sum_i \|V_i - V_k\|$$

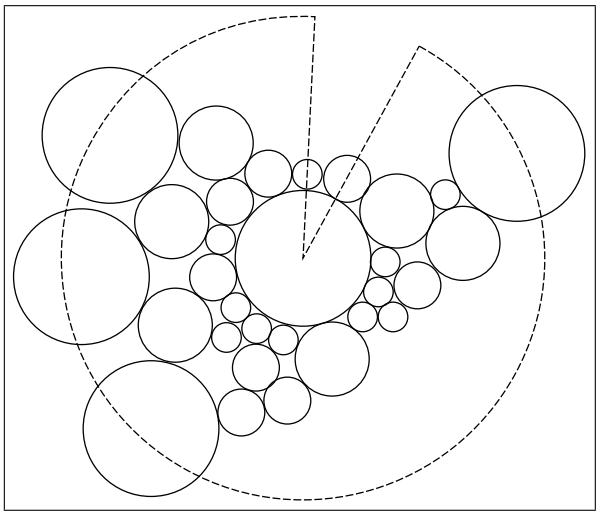

Figure 5. Example of an unspecified configuration: central larva has a high FoV value.

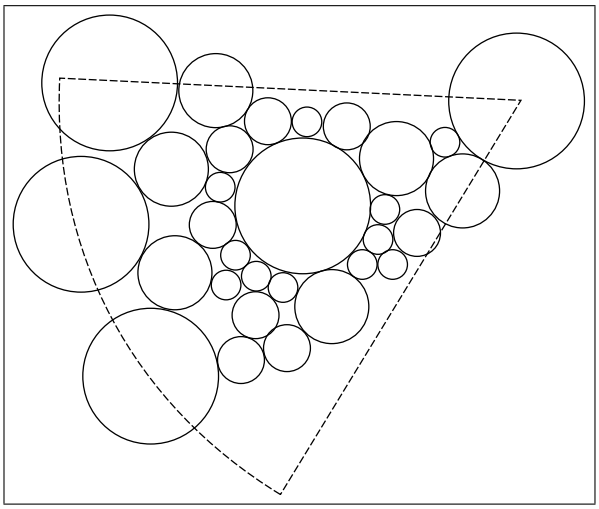

Figure 6. Example of an unspecified configuration: FoV value of peripheral larva is expected to be low.

This partial study allows us to forecast that minimal configurations for $S(V)$ give the brood an annular shape.

We stress the point that these conclusions are specific to the function S. If we assume, for instance, that the collective action (and the individual one, as we proved in section 2) of ants tends to minimize the surface occupied by larvæ, we do not observe concentric circles, but a dispersion of small items among large ones.

Thus, under the hypothesis that the action of ants minimizes the mutual distances between larvæ, we conclude that concentric annular sorting naturally arises.
In order to connect these minimal configurations to the ones observed in nature, we are to use realistic larvæ sizes and consider what actually happens in ant's nest. For the latter reason, we now introduce the notion of virtual size of an item.

3.3. Spacing and virtual size

Sendova-Franks et al. (2004) pointed out that larvæ, in a real brood, are far from each other, what allows ants to move everywhere in the brood. Moreover, the free space surrounding a larva generally increases with its size (Franks and Sendova-Franks, 1992). Following these observations, we define the virtual size of an item as its physical size added to the free space allocated to it by ants. Observations of Sendova-Franks et al. (2004) ensure that disparities between virtual sizes of items are, compared to their physical sizes, greatly stressed.
As a consequence, geometric configurations that minimize S can get through stochastic effects of the dynamical system. Thus, brood sorting is much closer to ideal annular configuration.
Furthermore, we are now able to explain the exceptional case of pupæ: when pupæ and prepupæ are present in the brood, they are located between the peripheral large larvæ and more central larvæ with medium size. Yet, pupæ and prepupæ are much bigger than larvæ that surround them. Following our analysis, this fact implies that virtual sizes of pupæ and prepupæ are similar to virtual sizes of surrounding larvæ. Consequently, we should observe that less free space is

allocated to pupæ and prepupæ. Indeed, this fact has been observed: Franks and Sendova-Franks (1992) showed that there is a positive correlation between individual space and metabolic rate and that pupæ and prepupæ do not require feeding but only grooming.
Our principle is therefore sufficient to explain the major causes of annular configuration, considering virtual sizes of objects rather than their physical sizes.

4. Conclusion and discussion

We have showed, in a mathematical way, that brood sorting can be explained without the help of swarm intelligence. We have also proved that it is achieved with drastically minimal hypothesis about ants' activity. Moreover, deducing a minimization principle, we believe that we have highlighted two of the major causes of the concentric annuli formation in *leptothorax unifasciatus* ant colonies, that is: almost minimization of the average of squared-distances between free larvæ, coupled with great differences between virtual sizes of brood items.
Even if we dropped the fascinating hypothesis of swarm intelligence, and only for this phenomenon of brood sorting, we can refer to the not less attractive concept of functional self-organization. A common self-organization deals with emergence of structures at a global level from interactions among lower-level components (**?**Nicolis and Prigogine, 1977). This concept is essential to handle more and more complex systems in biology. Beyond this subjective notion of self-organization, that is strongly related to the observer himself, the notion of functional self-organization which requires that the observed pattern is useful to individuals. For example, in the case of brood sorting, if we only observe concentric circles, it is really premature to invoke functional self-organization. We must consider those configurations as interesting ones, since we can recognize them as particular, but this is a subjective point of view: probably any other configuration, even not particular to our eyes, should be considered with equal attention. However, in the light of experiments of Francks and Sendova-Francks, we see that annular sorting is a functional phenomenon: on one hand, we have proved that annular sorting is achieved as soon as ants provide more space to larvæ that need more care, what involves only local criterions (there is no need to consider density of larvæ or more global notions). On the other hand, peripheral larvæ are, by a feed-back effect, more accessible to ants, so that the self-organization phenomenon has a direct influence on the care they receive from ants. The conjunction of these two phenomemons leads us to stand that annular sorting is a case of functional self-organization.

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